

THE MID-PROTEROZOIC LITTLE DAL MACROBIOTA, MACKENZIE MOUNTAINS, NORTH-WEST CANADA

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ABSTRACT. The Little Dal macrobiota is now known to comprise the previously reported carbonaceous megafossils *Chuaria circularis*, *Tawuia dalensis*, *Morania? antiqua*, and *Beltina danai*, as well as the following additional taxa: *Longfengshania stipitata*, *Grypania spiralis*, *Daltaenia mackenziensis* n.g. and sp., *Tyrasotaenia* sp., and *Tyrasotaenia?* sp. The dubiofossil '*Bergaueria?*' reported earlier is probably nonbiogenic.

Of special interest are three-dimensionally preserved specimens of *Chauria*, *Tawuia*, and *Tyrasotaenia?*, found associated with 'molar-tooth' structure. A carbonized test separates the pure, equigranular, microcrystalline calcite infilling of the fossil interior from an argillaceous carbonate matrix. This infilling is optically and chemically indistinguishable from that comprising the 'molar-tooth' structure. These relationships indicate comparable processes and timing for both fossilization of the organisms and filling of syneresis cracks during compaction and consolidation of the sediment.

THE first elements of the Little Dal macrobiota were discovered and collected by J. D. Aitken in 1976 while mapping the Proterozoic succession in the Mackenzie Mountains for the Geological Survey of Canada. The collection was enlarged during the following year and a preliminary report on this important find was published (Hofmann and Aitken 1979). The Little Dal biota, particularly the association of *Chuaria* and *Tawuia*, has since been recognized in approximately coeval rocks elsewhere, at localities in China (Xing 1979; Zheng 1980; Du 1982; Duan 1982), Svalbard (Knoll 1982), the Vindhyan of India, and in a second formation of the Little Dal Group (for summary, see Hofmann 1985). There can be little doubt that macroscopic organisms of as yet undetermined, but most likely eucaryotic, algal affinities were widespread in rocks of 1.0–0.7 Ga age. As more occurrences come to light we may see a trend leading to the eventual recognition of a distinct chronostratigraphic interval typified by this macrobiota, just as there are now proposals for establishing an Ediacaran/Vendian Period and System characterized by a unique soft-bodied metazoan fauna (Jenkins 1981; Cloud and Glaessner 1982; Sokolov and Fedonkin 1984). With the oldest structured, macroscopic carbonaceous remains (filaments in the Changcheng System of China) dating back to about 1.8 Ga (Hofmann and Chen 1981), and the presence of a macrobiota in the approximately 1.3 Ga old Greyson Shale of Montana (Walter, *et al.* 1976), the whole interval of the middle and late Proterozoic becomes a more and more attractive target in the search for evidence of macroscopic life. The purpose of this paper is to furnish data on new material from the Little Dal Group collected since the initial account was published. The collections here reported come from two formations at five localities in the Mackenzie Mountains, as shown in text-figs. 1 and 2; two of the localities (1 and 2) had previously yielded specimens (Hofmann and Aitken 1979).

The large number of specimens now available from the Little Dal Group demonstrate a simple gross morphology of the two predominant taxa, but they also exhibit some unusual preservational variants (Pls. 35–38), including three-dimensionally preserved forms. The latter are associated with 'molar-tooth' structure, thin crumpled sheets of calcite which are a characteristic feature of certain Helikian (mid-Proterozoic) carbonate sequences of North America (see Smith 1968; O'Connor 1972; Donaldson 1973). The identical nature of the distinct equigranular microcrystalline calcite filling of both fossil and 'molar-tooth' structures is helpful in elucidating both taphonomic aspects and the diagenetic history of this type of carbonate sediment, as discussed further on.

GEOLOGIC SETTING

The stratigraphy and sedimentology of the Little Dal Group is treated at some length by Aitken (1981). The group is part of the Mackenzie Mountains Supergroup and comprises an Helikian epicratonic sequence of stromatolitic dolostones, mature clastics, and evaporites. The approximately 2 km thick succession overlies quartzites of the Katherine Group, and underlies a regional unconformity, above which are volcanics and cupriferous dolostones of the Redstone River and Coppercap Formations, referred to by Aitken as the 'Copper cycle'. The latter rocks are themselves unconformably overlain by the late Proterozoic Rapitan Group, which includes widespread glaciogenic deposits and an iron-formation. The whole assemblage is allochthonous, having been thrust north-eastward further on to the North American craton during the Laramide orogeny, much like a similar package comprising the Purcell and Windermere Supergroups in the southern Canadian Cordillera.

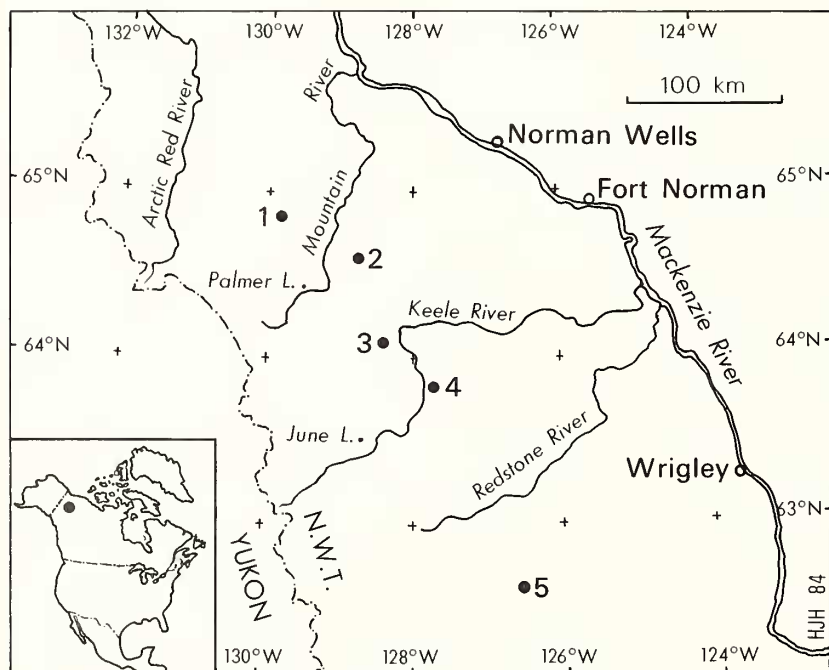
The Little Dal Group is divided into informally named lithostratigraphic units of formational rank, as shown in text-fig. 2, each reflecting a particular setting on the ancient craton. A regional multistage stromatolite buttress ('Rouge Mountain Member') in the lower part of the group separates a platform assemblage in the south-east from a basinal rhythmite assemblage in the north-western part of the area. The macrobiota is now known from both the basinal and the platform assemblages, as well as from the Rusty shale unit in the upper part of the group.

Locality details

The present study is based on new collections made by the writer at localities 1, 2, and 4, and on collections made by J. D. Aitken at localities 3 and 5. The localities are as follows:

Locality 1. $64^{\circ}48'N$, $129^{\circ}52.5'W$. (see Section 76AC-2 in Hofmann and Aitken 1979, figs. 1, 8; middle portion of Basinal assemblage).

Locality 2. $64^{\circ}37'N$, $128^{\circ}50'W$. (see Section 77AC-38 in Hofmann and Aitken 1979, figs. 1, 8; lower half of Basinal assemblage).



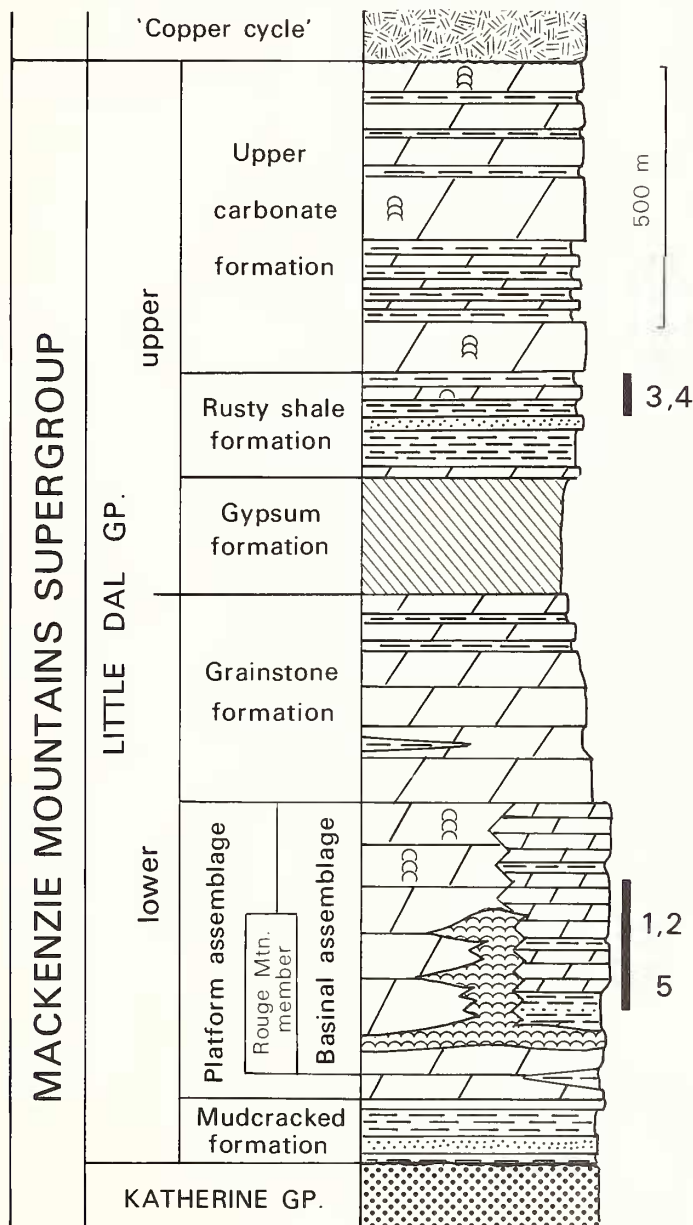
TEXT-FIG. 1. Map showing localities 1 to 5.

Locality 3. 64° 06' 25" N. 128° 27' 30" W. (see Section 77-36 in Aitken 1981, fig. 3.3, 3.17; Geol. Surv. Canada locality C85852, approximately 51·7 m below top of Rusty shale formation).

Locality 4. 63° 50' 20" N. 127° 33' 55" W., at an elevation of approximately 1170 m (see florencite locality illustrated photographically in Pouliot and Hofmann 1981; upper part of Rusty shale formation).

Locality 5. 62° 37' 31" N. 126° 36' 40" W. (see Section 79-2 in Aitken 1981, fig. 3.3, 3.12; Geol. Surv. Canada locality C85853, Platform assemblage, interval 238·3–260·5 m above base of section; in type section of Little Dal Group).

All specimens illustrated are deposited in the National Type-fossil Collection, Geological Survey of Canada, Ottawa, under the GSC accession numbers cited in each plate caption.



TEXT-FIG. 2. Generalized stratigraphic column for Little Dal Group (after Aitken 1981), showing two intervals with megafossils (vertical bar) and collecting localities 1 to 5.

SYSTEMATIC PALAEONTOLOGY

In the following section, full synonymies are not presented for each species. Instead, the reader is referred to recent papers citing synonymies.

As presently construed the Little Dal macrobiota comprises the following taxa:

INCERTAE SEDIS

Algae?

Tawuia dalensis Hofmann, 1979

Chuarina circularis Walcott, 1899

Longfengshania stipitata Du, 1982

Morania? antiqua Fenton and Fenton, 1939

Beltina danai Walcott, 1899

Daltaenia mackenziensis Hofmann, gen. et sp. nov.

Grypnaia spiralis Walter, Oehler and Oehler, 1976

Tyrasotaenia sp.

Tyrasotaenia? sp.

DUBIOFOSSILS, probably nonbiogenic

'*Bergaueria*?' Hofmann, in Hofmann and Aitken, 1979

Genus *TAWUIA* Hofmann, in Hofmann and Aitken, 1979

Type species. *Tawuia dalensis* Hofmann, in Hofmann and Aitken, 1979.

Tawuia dalensis Hofmann, in Hofmann and Aitken, 1979

Plate 35, figs. 1-3; Plate 36, figs. 1-5, 7-11; Plate 37, figs. 1, 2, 4-7; Plate 38, figs. 1-3; text-figs. 3, 4 (partim).

1977 *Fermoria* with 'filament', Sahni, pp. 293, 298.

1979 *Tawuia dalensis* Hofmann, in Hofmann and Aitken, pp. 157-160, figs. 13, 15, 16.

1979 *Shouhsienia shouhsienensis* Xing, p. 12, pl. 12, figs. 6-7 (nom. nud.).

1979 ?*Shouhsienia longa* Xing, p. 12, pl. 15, fig. 5 (nom. nud.).

1979 *Vendotaenia* sp. Xing, p. 12, pl. 12, fig. 9 (non 8).

EXPLANATION OF PLATE 35

Carbonaceous compressions and three-dimensionally preserved specimens of *Tawuia dalensis* Hofmann, *Chuarina circularis* Walcott, *Tyrasotaenia* sp., and *Tyrasotaenia? sp.*, all from locality 1.

Specimens in figs. 4, 8-10 from slab illustrated in text-fig. 4.

Fig. 1. Bedding surface showing highest observed concentration of carbonaceous compressions of *Tawuia dalensis* Hofmann. GSC 77176, $\times 1$.

Fig. 2. Association of *T. dalensis* Hofmann containing submillimetric discs, and *C. circularis* Walcott. Straight specimen at top is enlarged in fig. 6. GSC 77177, $\times 1$.

Fig. 3. Specimen of *T. dalensis* Hofmann with concentric terminal folds, most likely due to compaction. GSC 77178, $\times 2$.

Fig. 4. Three-dimensionally preserved specimens of *C. circularis* Walcott with surface indentations due to compaction, and nearby *Tyrasotaenia? sp.* GSC 77179, $\times 10$.

Fig. 5. Bedding surface showing dense population of *C. circularis* Walcott and short specimens of *Tawuia dalensis* Hofmann with axial marking. GSC 77191, $\times 1$.

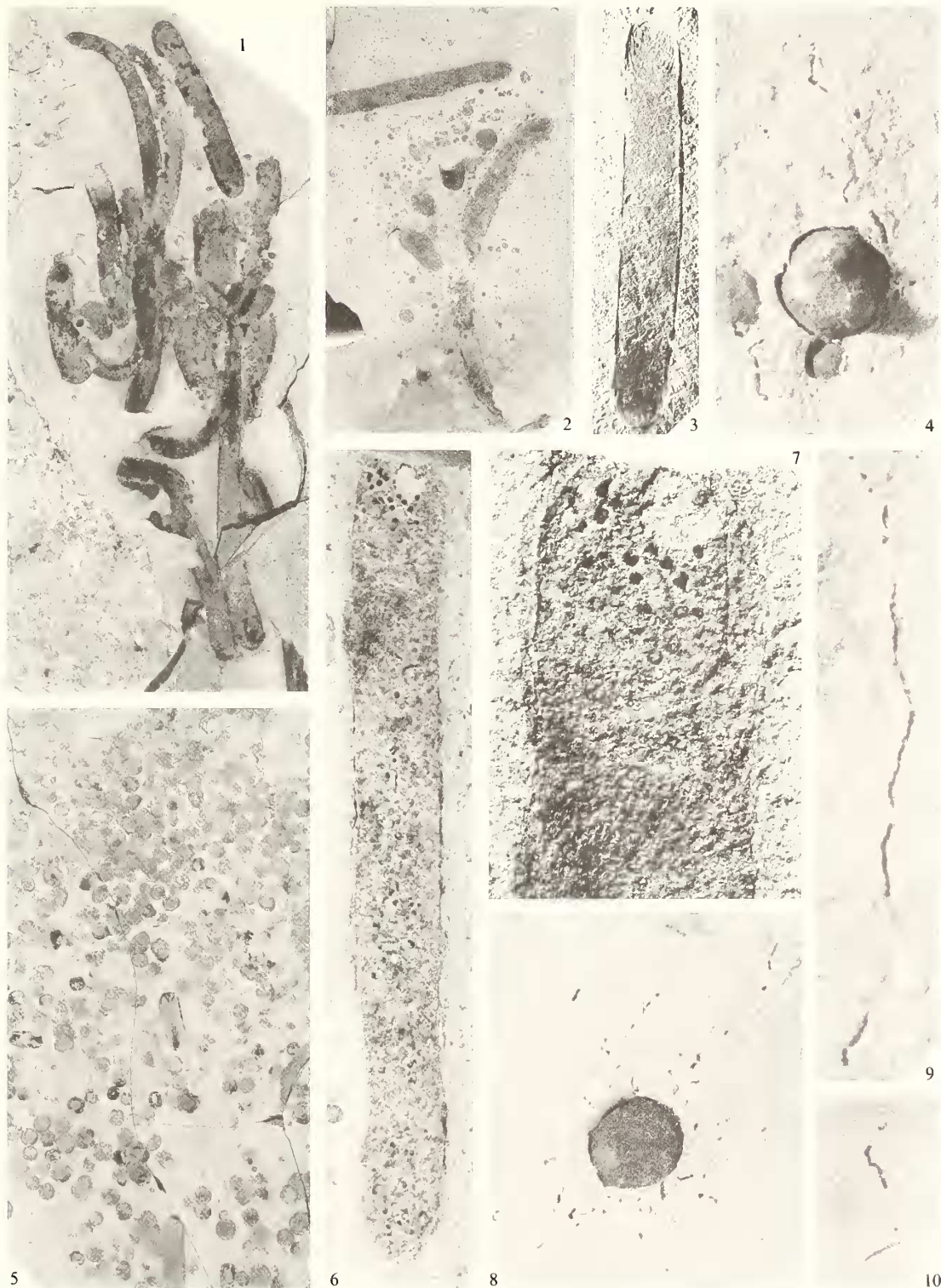
Fig. 6. Enlarged view of specimen at top of fig. 2, showing large number of submillimetric discs. GSC 77177, $\times 4$.

Fig. 7. Enlarged view of submillimetric discs in fig. 6. $\times 10$.

Fig. 8. Three-dimensionally preserved *C. circularis* with subradially oriented *Tyrasotaenia? sp.* GSC 77180, $\times 10$.

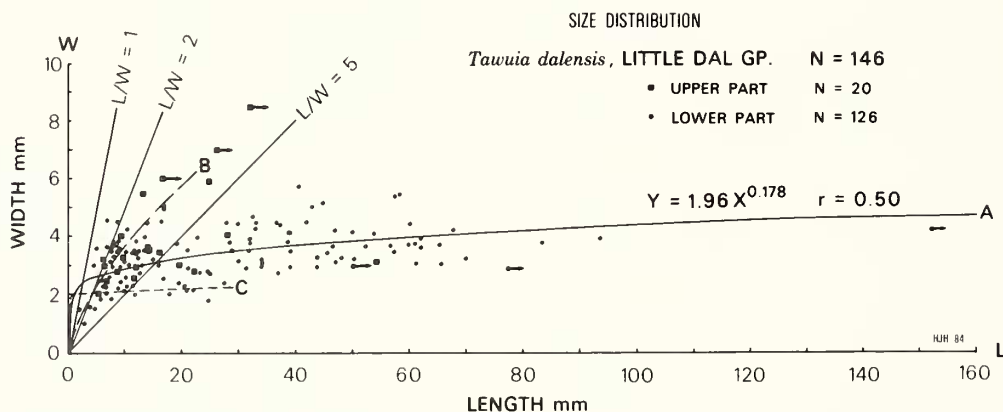
Fig. 9. Three-dimensionally preserved *Tyrasotaenia? sp.* GSC 77181, $\times 10$.

Fig. 10. Carbonaceous compressions of *Tyrasotaenia* sp. on same slab as fig. 9. GSC 77182, $\times 10$.



- 1980 *Tawuia* cf. *dalensis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 29.
 1980 *Tawuia* cf. *dalensis* Zheng, p. 64, pl. 2, fig. 29.
 1980 *Tawuia striatis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 28 (nom. nud.).
 1980 *Tawuia striatia* Zheng, pp. 63, 64, pl. 2, fig. 28.
 1980 *Tawuia* spp. Zheng in Yang *et al.*, p. 254, pl. 17, figs. 24–27.
 1980 *Tawuia* spp. Zheng, pl. 2, figs. 24–27.
 1980 *Ellipsophysa axicula* Zheng, in Yang *et al.*, p. 253, pl. 17, figs. 5, 6 (nom. nud.).
 1980 *Ellipsophysa axicula* Zheng, p. 60, pl. 1, figs. 5, 6.
 1980 *Ellipsophysa proceriaxis* Zheng, in Yang *et al.*, p. 254, pl. 17, figs. 11, 13, 15, (nom. nud.).
 1980 *Ellipsophysa proceriaxis* Zheng, p. 60, pl. 1, figs. 7, 13; pl. 2, figs. 11, 15.
 1980 *Pumilibaxa huaihoiana* Zheng, in Yang *et al.*, p. 254, pl. 17, figs. 9, 12, 32 (nom. nud.).
 1980 *Pumilibaxa huaiheiana* Zheng, p. 62, pl. 1, fig. 9.
 1980 *Nephroformia liulaobeiensis* Zheng, in Yang *et al.*, p. 254, pl. 17, fig. 31 (nom. nud.).
 1980 *Nephroformia liulaobeiensis* Zheng, pp. 62–63, pl. 1, fig. 31.
 1982 *Shouhsienia shouhsienensis* Du (partim), p. 3, figs. 6, 10.
 1982 *Shouhsien longa* Du, p. 3, fig. 9 (nom. null.).
 1982 *Tawuia dalensis* Duan, p. 63, fig. 5K–N.
 1982 *Tawuia sinensis* Duan, pp. 63–64, figs. 3K–Q, 5P(partim), 6.
 1982 *Tawuia dalensis* Knoll, p. 275, text-fig. 3; pl. 3, figs. 13, 14.
 1985 *Tawuia dalensis* Hofmann, fig. 4.

Description. Taxon characterized by straight and curved, roundly terminated tomaculate (sausage-shaped) objects, 1–8.5 mm wide (mean width = 3.42 mm; $\sigma = 1.03$ mm; $N = 146$), and generally several centimetres long (mean length = 25.44 mm; $\sigma = 22.30$ mm; $N = 146$), mostly with an aspect ratio (length/width) between 2 and 5 (text-fig. 3), the longest specimen (incomplete) with a length of 15.2 cm (Pl. 38, fig. 1). The specimens isolated as well as clustered, closely associated with abundant *Chuaria*, both preserved either as lustrous black or greenish carbonaceous compressions, as impressions if carbonaceous film absent, and, rarely, as three-dimensional objects. The outline generally smooth and even, although various kinds of folds may be present; the sides parallel to slightly tapering in short individuals, termini hemispherical or semicircular, rarely slightly pointed. In some specimens a disc-like terminal structure visible (Pl. 35, fig. 3; Pl. 36, figs. 1, 11), while in others a



TEXT-FIG. 3. Bivariate plot of size distribution of *Tawuia dalensis* Hofmann in Little Dal Group. Points with arrows indicate minimum lengths of incomplete specimens. Compilation includes the eighteen data points reported by Hofmann and Aitken (1979, fig. 15). Geometric regression lines added for comparison; A, *T. dalensis*, Little Dal Group; B, *T. dalensis*, Kapp Lord Farm, $Y = 0.73X^{0.692}$, $N = 125$ (Knoll 1982, text-fig. 3); C, *T. sinensis* Duan, Liulaobei Farm, $Y = 1.97X^{0.035}$, $N = 33$, $r = 0.08$ (Duan 1982, text-fig. 6). Aspect ratio lines (L/W) are also plotted to show concentration of specimens in region with L/W between 2 and 5.

dark axial or off-axial zone present (Pl. 35, fig. 5; Pl. 36, fig. 8), both possibly artifacts of preservation. Morphologic variability broad, including I-, J-, C-, U-, S-shaped, and open spiral forms, with a preference for rectilinearity, particularly in short individuals. The widest forms occurring in the Rusty shale unit, a black shale in which the flattening of the cylinders has been more extensive than in the dolomitic rhythmites of the lower part of the Little Dal Group, in which occur even three-dimensionally preserved specimens.

Certain rare specimens exhibiting numerous scattered small black discs (pyritic?), uniformly about 0.2 mm across (Pl. 35, figs. 6, 7). Three-dimensionally preserved specimens associated with 'molar-tooth' structure (text-fig. 4), and showing opaque, disrupted walls, about 1 μm thick, of black kerogen with patterns of cracks due to syneresis or displacement by crystal growth (Pl. 37, fig. 5). The fossils filled with clear, pure (based on electron microprobe analysis), xenotopic, equigranular calcite (microspar?) that weathers to a medium bluish grey colour and has a grain size of about 10 μm . The matrix surrounding the fossils heterogeneous and darker, dolomitic and argillaceous, finely laminated, buff weathering, and characterized chemically by abundant K, Al, Si, Mg, and Ca.

Occurrence. Localities 1-5.

Discussion. The new material provides a basis for further insight into aspects of *Tawuia* biology, taphonomy, and nomenclature, but also leaves certain questions unresolved. First, several specimens have large numbers of submillimetric discs of uniform size (Pl. 35, figs. 6, 7). These are of considerable interest because they may provide a possible link between *Tawuia* and *Chuarua*, and relate them to the algae. Such a relationship has been inferred on the basis of the close association of isolated specimens of both taxa, and the seemingly gradational size and shape variation between the two (Hofmann 1981, p. 421; Duan 1982). If the minute discs are not diagenetic artifacts, which remains an alternative, they could be interpreted as reproductive structures. One can only speculate if, after release from *Tawuia*



TEXT-FIG. 4. Slab with three-dimensionally preserved specimens of *Tawuia dalensis*, *Chuarua circularis*, and *Tyrasotaenia?* sp., and 'molar-tooth' structure (dark linear pattern); $\times 0.42$. Specimens of 'molar-tooth', *Chuarua*, and *Tawuia* in lower right corner of slab are shown in vertical section in Plate 37, fig. 1; specimen in upper left corner shown in Plate 36, fig. 10 and Plate 37, fig. 4.

individuals these could have grown, first isometrically to millimetric spheroids, and subsequently by allometric growth to the *Tawuia* stage, as suggested by data in text-fig. 3.

One difficulty with this hypothesis is that there are many more known occurrences of *Chuarua* than of *Tawuia* (Hofmann 1985, fig. 3). Another is the unique occurrence of a linear array of identically sized, and possibly consanguineous, overlapping discs of *Chuarua* from the 850 Ma old Uinta Mountain Group (Hofmann 1977, fig. 2a). This string of discs, if indeed consanguineous, would also disallow the idea of a postulated *Chuarua*-*Tawuia* relationship.

The nature and function of the disc-like terminal structure (Pl. 35, fig. 3; Pl. 36, figs. 1, 11) remain obscure. It may be a purely preservational artifact resulting from the compression of a roundly terminated cylinder with a resistant, pliable membrane, like longitudinal, oblique, and concentric wrinkles such as shown in Plate 36, fig. 1. The tapering of other specimens, particularly the more tightly bent ones (Pl. 36, fig. 3), may represent cylinders already partially deflated at the time of embedding, or abnormal specimens.

The axial to off-axial stripe of a number of specimens is more problematical. The possibility that the stripe, because of its position, might represent an alimentary canal, and the organism a metazoan, has been considered and rejected for lack of compelling evidence. The carbonaceous composition combined with the lack of any recognizable body opening, which should be of corresponding size, or other identifiable organs (e.g. structures indicating musculature or active motility), make such an interpretation difficult.

The three-dimensional preservation of *Tawuia* (and *Chuarua*) specimens indicates a heterogeneous constitution for the organisms, with a resistant test and a readily decomposed interior that is replaced by calcite. The close association of three-dimensionally preserved, calcite-filled specimens and crumpled planar features ('molar-tooth' structure) filled with identical equigranular microcrystalline calcite is noteworthy (Pl. 37, fig. 1; text-fig. 4). The black, kerogenous envelope outlining the fossils is absent in the 'molar-tooth' structure, a significant difference. Both types of structure reflect similar peculiar diagenetic conditions, and they bear on the controversial origin of 'molar-tooth' structure,

EXPLANATION OF PLATE 36

Carbonaceous compressions and three-dimensionally preserved specimens of *Tawuia dalensis* Hofmann (figs. 1-5, 7-11), *Chuarua circularis* Walcott (figs. 6, 12), and *Tyrasotaenia?* sp. (fig. 12).

Specimens in Figs. 4-7, 9, 10, 12 all on slab shown in text-fig. 4.

Fig. 1. *T. dalensis* Hofmann; clustered specimens showing various types of wrinkles. Locality 3. GSC 77192, $\times 4$.

Fig. 2. *T. dalensis* Hofmann; specimen with granulate markings. Locality 4. GSC 77193, $\times 4$.

Fig. 3. *T. dalensis* Hofmann; strongly tapering, curved specimen. Locality 1. GSC 77194, $\times 4$.

Fig. 4. *T. dalensis* Hofmann; U-shaped specimen preserved three-dimensionally, showing round, uncompressed termini. Locality 1. GSC 77183, $\times 4$.

Fig. 5. *T. dalensis* Hofmann; uncompressed, slightly tapered, with *Tyrasotaenia?* sp. at one end. Locality 1. GSC 77184, $\times 4$.

Fig. 6. *C. circularis* Walcott; three-dimensional specimen with indentations due to burial. Locality 1. GSC 77185, $\times 4$.

Fig. 7. *Tawuia dalensis* Hofmann; three-dimensional, C-shaped specimen with medial, longitudinal fold. Locality 1. GSC 77186, $\times 4$.

Fig. 8. *T. dalensis* Hofmann; U-shaped compression with axial marking. Compare with fig. 7. Locality 1. GSC 77195, $\times 4$.

Fig. 9. *T. dalensis* Hofmann; tapering, three-dimensional specimen with collapsed central region. Compare with *Pumilibaxa huaiheiana* Zheng. Locality 1. GSC 77187, $\times 4$.

Fig. 10. *T. dalensis* Hofmann; U-shaped specimen with oblique fold, shown in thin section view in Plate 3, figs. 4-6. Locality 1. GSC 77188, $\times 4$.

Fig. 11. *T. dalensis* Hofmann; coiled specimen with terminal disc. Locality 1. GSC 77196, $\times 4$.

Fig. 12. *C. circularis* Walcott overlain by thin layer of matrix with cross-sections of specimens of *Tyrasotaenia?* sp. Locality 1. GSC 77189, $\times 10$.



discussed by Smith (1968) and O'Connor (1972). Both authors favoured a biogenic origin for this phenomenon, citing in evidence the occasional close association with stromatolites, and the presence of cell remains in some 'molar-tooth' sheets (O'Connor 1972, p. 606). The evidence for a biological contribution is, nevertheless, circumstantial and weak, and the purported microbes may be accidentally lodged in the cracks without playing a constructive role in its formation. The angulate patterns of the contorted thin vertical sheets indicate that a mechanical explanation (syneresis) is to be sought to explain the Little Dal 'molar-tooth' structures, such as mineral-filled cracks forming under water at the limits of influence of competing small, equally spaced tension domains, analogous to those resulting in the development of contraction cells in the formation of mudcracks or columnar basalt.

The considerable compaction indicated by the crumpled planar features (Pl 37, fig. 1), the relative lack of compaction of the fossils, and the identical nature of the equigranular microcrystalline calcite fillings, all indicate that the fillings in both are an early diagenetic phenomenon: three-dimensional shapes are chemically filled, providing some rigidity to them, before substantial compaction of the less rigid surrounding sediment occurred. The still-intact walls of the entombed organisms prevented the mechanical entry of impurities, whereas the voids created by inferred syneresis cracking provided loci for precipitation resulting in 'molar-tooth' structure. Conditions of unusual concentration of certain ions may have been a factor involved in this precipitation: elevated salinity, organic compounds, and carbonate gels come to mind. Little is known about carbonate gels, and they seem unlikely, considering the ease of crystallization of CaCO_3 , but reference to them has been made by Lebedev (1967, pp. 24–29). As the sediment compacted (more than 50%, judging from the shortening shown in Pl. 37, fig. 1), the more rigid, vertically extensive, tabular struts of the 'molar-tooth' structure were crumpled, resulting in the disharmonic folds (reminiscent of ptygmatic folds in migmatites). By comparison the very limited vertical extent of the fossils resulted in little or no perceptible disharmonic folding during compaction, leaving the shapes much as they were at the time of burial, and probably in life. The timing of the filling by equigranular microcrystalline calcite, and the composition and physical properties of the surrounding, dewatering matrix were crucial elements whose combination resulted in such extraordinarily well-preserved Proterozoic macrofossils and this type of 'molar-tooth' structure.

EXPLANATION OF PLATE 37

All specimens are thin section views of specimens in slab illustrated in text-fig. 4. Locality 1.

Fig. 1. *Tawuia dalensis* Hofmann (upper right), *Chuaria circularis* Walcott (top middle), and 'molar-tooth' structure (left). Vertical thin section of lower right extremity of slab in text-fig. 4. The compaction of the finely laminated sediment indicated by the ptygmatic crumpling of the 'molar-tooth' structure is at least 50%. Locality 1. GSC 77190, $\times 5$.

Fig. 2. Enlarged view of upper left of fig. 7, showing detail of *Tawuia* wall separating fill and matrix. $\times 200$.

Fig. 3. Enlarged view of 'molar-tooth' structure (uppermost left portion of fig. 1), showing absence of black film between calcite fill and matrix. $\times 50$.

Fig. 4. *T. dalensis* Hofmann. Thin section of specimen in Plate 36, fig. 10, illustrating folds, preservation of carbonaceous wall, clear calcite (microspar?) fill, and heterogeneous matrix. $\times 5$.

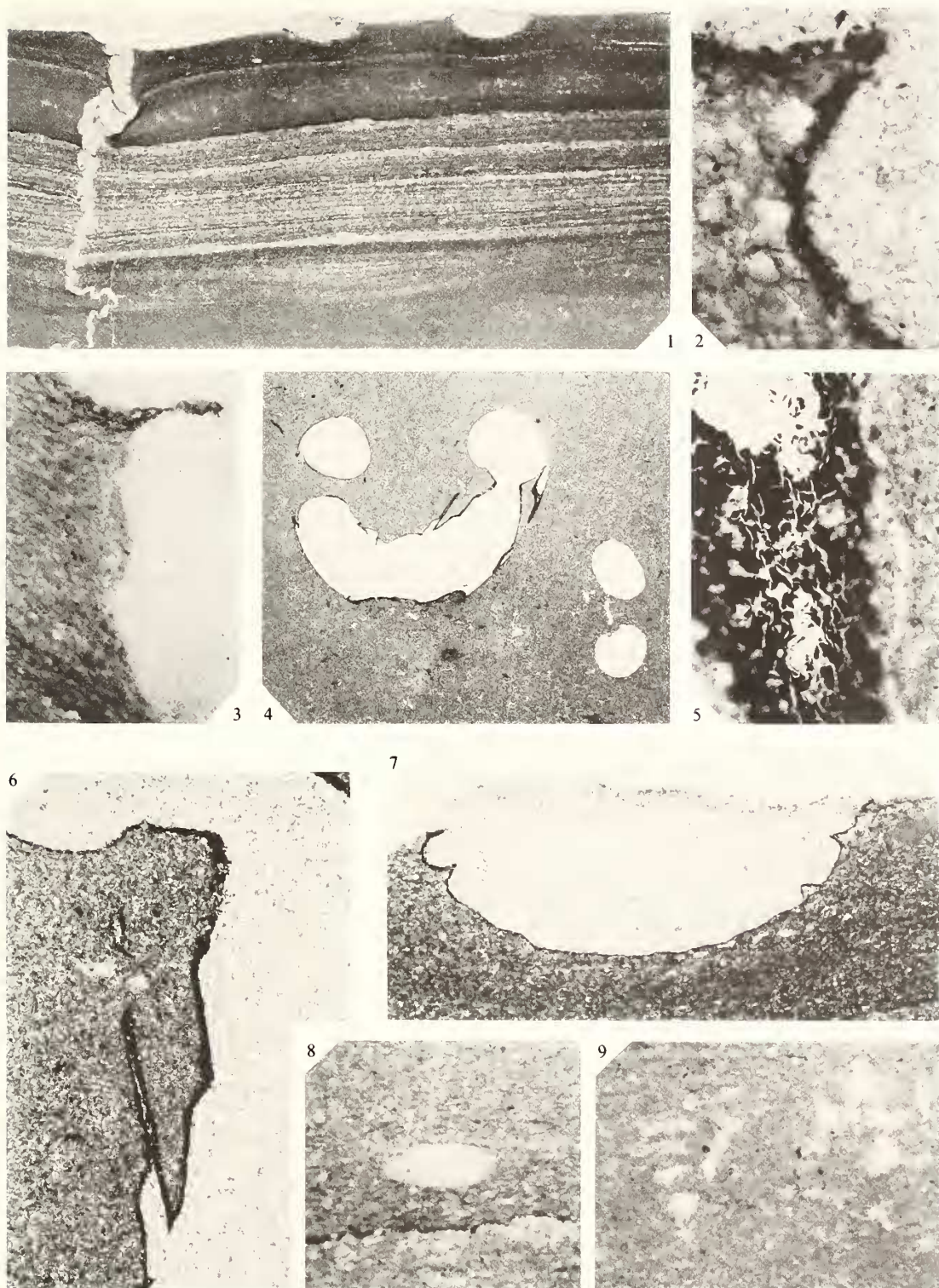
Fig. 5. Enlarged view of plunging fold at upper right of specimen in fig. 4, illustrating the cracked nature of the black wall material in tangential view of wall. $\times 125$.

Fig. 6. Enlarged view of plunging fold near middle of specimen in fig. 4, showing nature of wall and contrast between clear calcite fill and matrix. $\times 25$.

Fig. 7. Enlarged view of *Tawuia* specimen at upper right of fig. 1, showing folds in the wall in vertical section. GSC 77190a, $\times 25$.

Fig. 8. *Tyrasotaenia?* sp. Enlarged view of cross-section of specimen near top middle of fig. 1, to the left and below *Chuaria* specimen. GSC 77190b, $\times 50$.

Fig. 9. Calcite-filled voids, possibly *Tyrasotaenia?* sp. Enlarged view of portion just below *Tawuia* specimen at upper right of fig. 1. $\times 50$.



Finally, the nomenclatorial aspect of these tomaculate fossils needs to be discussed. Since the name *Tawuia* was introduced in 1979, several occurrences have been reported from other parts of the world, and a great number of new taxa have been erected (see synonymy). Three species of *Tawuia* are now named: *T. dalensis*, *T. striatia*, and *T. sinensis*. [See Note 1 added in proof, p. 353.]

T. striatia is said to be distinguished from the type species, *T. dalensis*, only by the absence of a terminal disc and by the presence of longitudinal striations. Zheng (1980) commented on the possible synonymous nature of the two species, but preferred to regard them as separate, considering the striations to be superficial features, and the terminal disc an internal structure. He did not state how many specimens were seen, and illustrated only one. Considering the wide shape (= preservational) variability among a large number of specimens of *T. dalensis*, which includes material with characteristics that could be attributed to *T. striatia*, the preferred interpretation here is to regard these two species as synonymous.

T. sinensis is reported to be somewhat narrower, shorter, and straighter than *T. dalensis* (Duan 1982), with widths averaging about 2 mm, and ranging between 1.6 and 3.5 mm, and lengths up to 29 mm. Nevertheless, the size distribution of thirty-three specimens from the Liulaobei Formation, as plotted by Duan (1982, fig. 6), is overlapped by that of *T. dalensis* from the Little Dal Group shown in text-fig. 3. Curved specimens from the same formation were assigned by Duan to *T. dalensis*. However, curvature is most likely an accidental, preservational feature rather than a biologic one, as demonstrated by specimens in the present material that includes a wide range of intermediate curvatures. *T. sinensis* can thus also be considered as probably synonymous with *T. dalensis*.

Type specimens of the other, genus-level taxa reported from Asia, and listed in the synonymy, were not seen; neither was type material of *T. dalensis* seen when those taxa were erected. Judging from the illustrations and translations of descriptions in the literature, and considering the overlapping size ranges, the great variety of preservational variants and allometric relationship of length to width exhibited by type material of *T. dalensis* from the Mackenzie Mountains, it is difficult to make distinctions between the taxa, and all those that are listed above are regarded as probable synonyms. Examples of any one of these can be seen in the present material. What is clear is that, regardless of what name has been used, the large tomaculate fossils in Asia, North America, and Europe represent a distinct group, probably of eucaryotic algae that constituted part of a widespread mid- to late Proterozoic marine macroplankton.

Before concluding this discussion, one should also mention, however, the occurrence of dark brown and black tomaculate fossils of strikingly similar size and aspect (15–25 mm by 1.8–2.5 mm), but with distinct, equally-spaced, narrow transverse markings (8–10 per mm). These are found in the Sinian System of the Shouhsien area in Anhui Province, China. They are referred to the genus *Sinosabellidites* Zheng and are assigned to the Pogonophora (Zheng 1980, p. 63). It would be interesting to determine whether the striking resemblance is merely fortuitous, or whether there could be a closer biologic affinity between *Tawuia* and *Sinosabellidites*. The latter alternative would require a rethinking of the algal interpretation for *Tawuia*, whose axial marking would assume more importance. Until more conclusive evidence for or against such a connection is developed, *Tawuia* is here regarded as distinct, and probably algal in nature.

Genus CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

Chuaria circularis Walcott, 1899

Plate 35, figs. 2, 4, 5, 8; Plate 36, figs. 6, 12; Plate 37, fig. 1 (partim); Plate 38, fig. 4 (partim);
Plate 39, fig. 2 (partim); text-fig. 4 (partim)

Synonymy. See Duan (1982, p. 59) and Hofmann (1977, table 1).

Description. Black, carbonaceous discs with concentric wrinkles, and, less commonly, linear folds; also as impressions when film absent, and as three-dimensionally preserved oblate spheroids with

accidental indentations; diameter submicroscopic to 4.5 mm; carbonaceous test of three-dimensional forms of the order of 1 μ m thick extensively cracked, separating homogenous equigranular microcrystalline calcite fill from finely laminated, heterogeneous matrix.

Discussion. The mode of preservation and occurrence of *Chuaria* specimens are identical to that already discussed under *Tawuia*, and the comments made there, and the discussion about possible mutual affinities between them, need not be repeated here.

Genus LONGFENGSHANIA Du, 1982

Type species. *Longfengshania stipitata* Du, 1982.

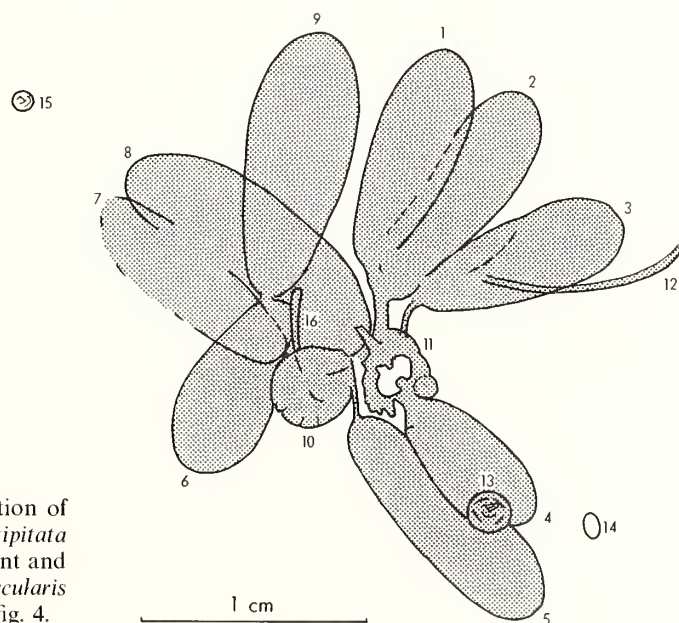
Longfengshania stipitata Du, 1982

Plate 38, fig. 4; text-fig. 5

Description. Bundles, elongate oval carbonaceous films with subradial arrangement, on bedding plane of black phosphatic and pyritic shale; compressions smooth and even, 8–12 mm long by 4 mm wide ($N = 9$); narrower, proximal end of oval film extending into a stalk-like projection or stipe, 0.5 mm or less wide and about 1 mm long. Stipes of adjoining specimens (nos. 1–4 in text-fig. 5) merging into a common, small, irregular, round carbonaceous mass several millimetres in diameter. Some ovals (nos. 1–2 in text-fig. 4) appearing to emanate from a common stipe; other individuals preserved only by partial marginal outline superimposed on more complete films (nos. 12, 16 in text-fig. 5). Specimens associated with *C. circularis* (nos. 13, 14?, 15 in text-fig. 5).

Occurrence. Locality 4.

Discussion. The structures are hardly distinguishable from those described by Du (1982) under *L. stipitata*, but they have a clustered appearance, and a subradial arrangement, with an apparent origin at a common central carbonaceous mass. The latter feature is of unusual interest, inasmuch as it suggests that the taxon represents a colony of a rather complex organism for its age, possibly an alga of phaeophyte or rhodophyte affinities, with an organ of attachment for the elongate oviform structure, somewhat like the modern *Halosaccion*.



TEXT-FIG. 5. Drawing showing interpretation of bundled specimens of *Longfengshania stipitata* Du (1–12) exhibiting subradial arrangement and superposition, and associated *Chuaria circularis* Walcott (13–15); compare with Plate 38, fig. 4.

However, before such an interpretation can be accepted, it is necessary to demonstrate beyond question that the stipe-like features are actually part of the oval compressions, and not due to fortuitous superposition of partial marginal outlines of unstiped bodies such as *Tawuia*. The latter possibility is suggested by the relationship between individuals 3 and 12 in text-fig. 4. It has not been possible to clarify this relationship for the present material, given the thinness of the films and the nature of the preservation. The type material of *L. stipitata* should be re-examined with this alternative interpretation for the stipes in mind. In fact the illustration of at least one specimen (fig. 11 of Du 1982) appears to show the stipe continuing across the oval film, curving towards the left as it crosses. Nevertheless, the close clustering of the individuals of similar size, and thus at a similar ontogenetic stage of development, and particularly their subradial orientation, with stipes towards the centre, suggest first, that a colony of stalked oviform bodies is a reasonable interpretation for now, and, secondly, that *Longfengshania* is a distinct genus.

Genus MORANIA Walcott, 1919

Type species. Morania globosa Walcott, 1919.

Morania? antiqua Fenton and Fenton, 1937

Synonymy. See Hofmann and Aitken (1979, pp. 160–162).

Description. Black, round carbonaceous films, with elliptical, ovate, or kidney-shaped outlines, without ornamentation, 2–11 mm across.

Discussion. Only a few specimens were seen in the present collection, so there is little new that can be added to the discussion in Hofmann and Aitken (1979). The structures may be a separate taxon, or represent compressions of globoid colonies of procaryotes.

Genus BELTINA Walcott, 1899

Type species. Beltina danai Walcott, 1899.

Beltina danai Walcott, 1899

Plate 39, figs. 5–8

Synonymy. See Hofmann and Aitken (1979, pp. 162–163).

Description. Carbonaceous films, fragmented, dark, irregular, unornamented; also smooth, brown impressions where film absent; outline irregularly angulate to smooth, oblong to equidimensional, from millimetric up to 3×8 cm in size; abundant on some bedding planes.

Occurrence. Localities 1 and 2.

EXPLANATION OF PLATE 38

- Fig. 1. Longest known specimen (an impression) of *Tawuia dalensis* Hofmann. Locality 1. GSC 77197, $\times 1$.
 Fig. 2. *T. dalensis* Hofmann; short, pitted specimen. Locality 4. GSC 77198, $\times 4$.
 Fig. 3. *T. dalensis* Hofmann; short specimen with transverse marks. Locality 4. GSC 77199, $\times 4$.
 Fig. 4. *Longfengshania stipitata* Du and *Chuarina circularis* Walcott. Compare with text-fig. 5. Locality 4. GSC 77200, $\times 4$.
 Figs. 5–6. '*Bergaueria?*' Hofmann, in Hofmann and Aitken. Structures probably inorganic, due to sapping. Locality 2. 5, GSC 77201, $\times 1$. 6, GSC 77202, $\times 1$.



HOFMANN, *mid-Proterozoic macrofossils*

Discussion. The new material here illustrated contains fragments much larger than those previously reported from the Little Dal Group. It considerably increases the known maximum size of the parent bodies from which the fragments are derived. The taxon represents fragments of thalli, of colonies, or of organic mats. Unfortunately, the new specimens provide no further clues as to their biologic affinities.

Genus *DALTAENIA* gen. nov.

Type species. *Daltaenia mackenziensis* sp. nov.

Diagnosis. Slender, broadly curvilinear, untwisted ribbon-like structures, of uniform submillimetric to millimetric width and centimetric length; apparent infrequent lateral branching.

Etymology. Named for its occurrence in the Little Dal Group, and its ribbon-like appearance (from the Greek *taenia*, meaning ribbon).

Daltaenia mackenziensis sp. nov.

Plate 39, figs. 1–3; text-fig. 6

Diagnosis. Qualitatively, as for genus. Ribbons 0.3–1.5 mm wide.

Type specimens. Holotype: GSC 77203, specimen No. 12 in Plate 39, figs. 2, 3, and text-fig. 6; paratypes: all other numbered specimens.

Etymology. Named for its occurrence in the Mackenzie Mountains (also located in the District of Mackenzie, in the Mackenzie Mountains Supergroup).

Type locality. Section 76AC-2 in fig. 4 of Hofmann and Aitken (1979, p. 154), from interval 20 to 30 m above locality C73715.

Type lithology and horizon. Laminated, grey calcareous dolosiltite, in basinal rhythmite assemblage of Little Dal Group.

Occurrence. Locality 1.

Description. Slender, ribbon-like structures on bedding planes, partially preserved as black carbonaceous or pyritized compressions, or, where film absent, as light yellowish-grey impressions in medium grey, laminated dolosiltite; associated with abundant, similarly preserved discs of *C. circularis*. Ribbons not twisted nor tightly bent, some apparently branching (e.g. Nos. 12–13, 12–14, 12–15, 26–27 in text-fig. 6), others definitely crossing (Nos. 17–18, 29–30). Width of individuals mostly

EXPLANATION OF PLATE 39

Figs. 1–3. *Daltaenia mackenziensis* gen. et sp. nov. For enumeration of specimens see text-fig. 6. Locality 1.

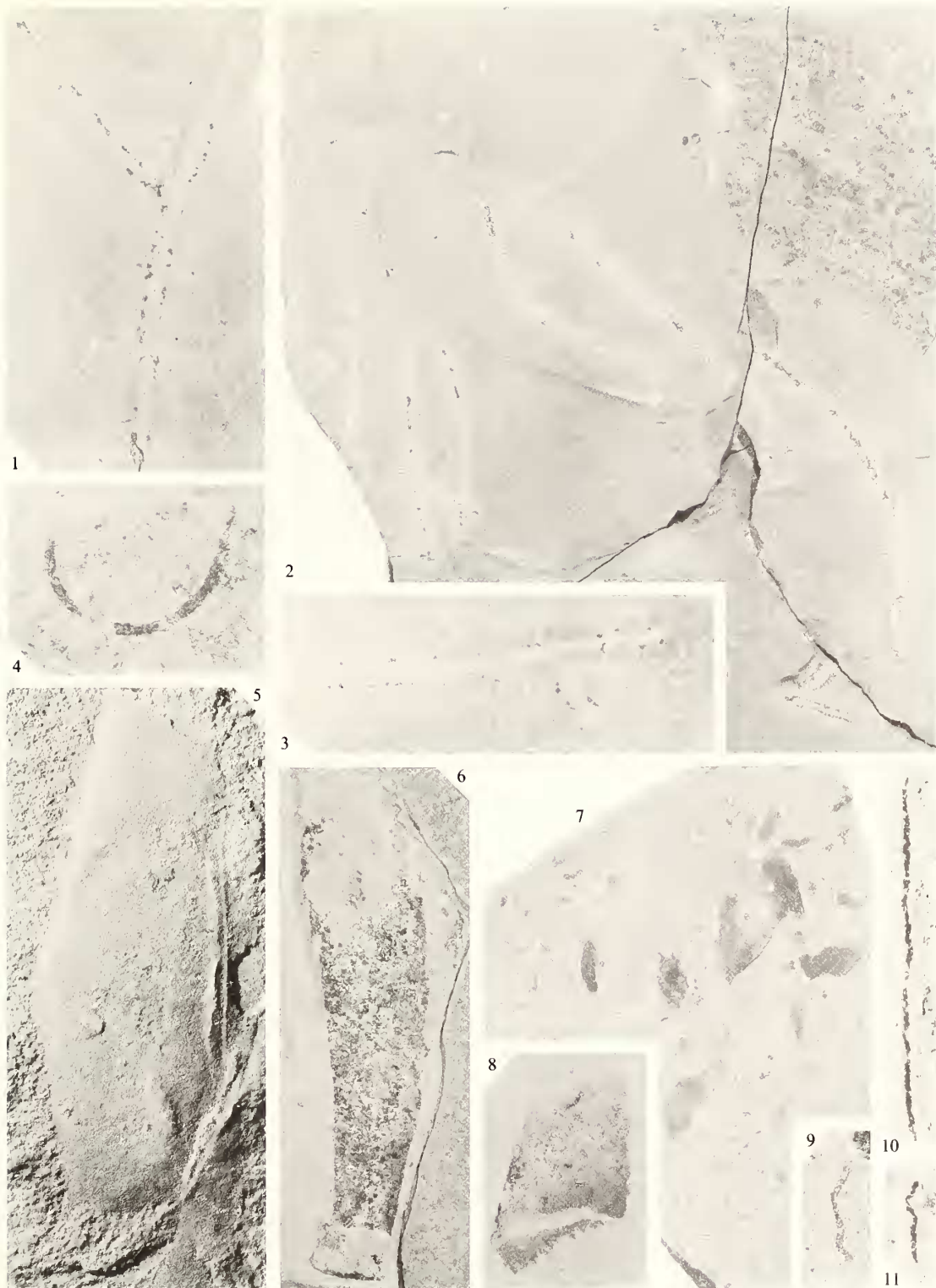
GSC 77203. 1, upper left portion of fig. 2, showing nature of junction of specimens 29 and 30, $\times 4$. 2, general view showing preferred orientation of specimens, and abundant small *Chuarina* in upper right of slab, $\times 1$.

3, portion of holotype, with possible branching, $\times 4$.

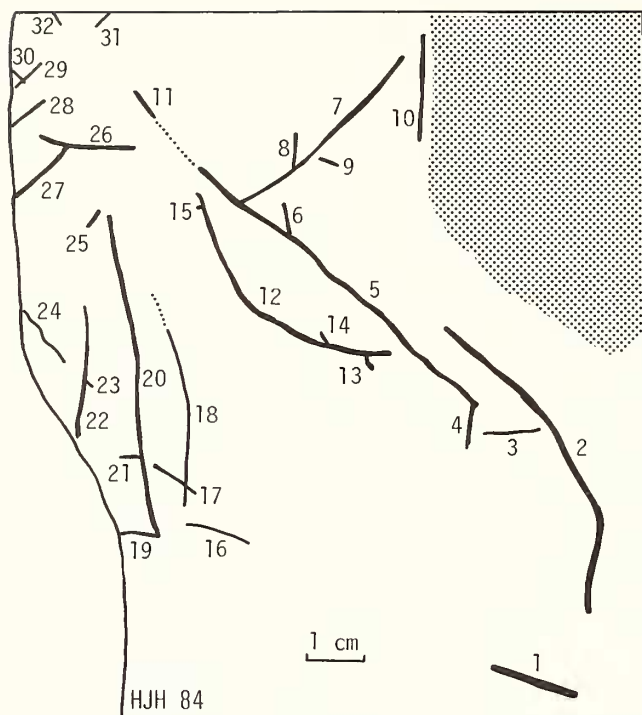
Fig. 4. *Grypania spiralis* Walter *et al.* Locality 1. GSC 77204, $\times 4$.

Figs. 5–8. *Beltina danai* Walcott. 5, largest known specimen. Locality 1. GSC 77205, $\times 1$. 6, second largest specimen. Locality 2. GSC 77206, $\times 1$. 7, scattered fragments, more typical of preservation. Locality 1. GSC 77207, $\times 1$. 8, angulate fragments. Locality 2. GSC 77208, $\times 1$.

Figs. 9–11. *Tyrasotaenia* sp. Carbonaceous fragments of filaments. 9, Locality 2. GSC 77209, $\times 10$. 10, long specimen. Locality 1. GSC 77210, $\times 10$. 11, short fragment. Locality 1, GSC 77211, $\times 10$.



HOFMANN, *mid-Proterozoic macrofossils*



TEXT-FIG. 6. Drawing of specimens of *Daltaenia mackenziensis* gen. et sp. nov., showing numbered specimens discussed in text; compare with Plate 39, fig. 2. Stippled area contains abundant *Chuaria circularis*.

uniform, ranging from 0.3 to 1.5 mm (mean = 0.64 mm; $\sigma = 0.29$ mm; $N = 32$) and length of fragments from 1 to 63 mm (mean 15.8 mm). Longest structures showing some subparallel orientation, suggesting active bottom currents at time of deposition. No surface ornamentation recognized.

Discussion. The evidence for the branching nature is inconclusive. No junction definitely attributable to branching was seen. However, of the thirteen junctions preserved, as shown in text-fig. 6 (4-5, 5-6, 5-7, 7-8, 12-13, 12-14, 12-15, 17-19, 19-20, 20-21, 22-23, 26-27, and 29-30), only two (17-18 and 29-30) are clearly crossovers, leaving eleven others, some of which could be attributed to branching (12-13 looks the most convincing). These ribbons are evidently much narrower and more slender than *Tawuia*. Comparable ribbons from the Proterozoic are *Proterotainia* (Walter *et al.* 1976), represented by two species in the Helikian Belt Supergroup of Montana, and *Tyrasotaenia* (Gnilovskaya 1971) from the Vendian of eastern Europe.

Proterotainia comprises unbranched, more or less straight (may be folded), ribbon-like carbonaceous films on bedding planes, 0.1-2.0 mm in width and up to 12.5 cm or more in length; longitudinal fibrillar structure may be present. Compared to the newly reported structures, *Proterotainia* specimens show a greater degree of flexibility, including some hairpin bends.

The Vendian *Tyrasotaenia*, also unbranched, is more twisted and crumpled, and somewhat narrower, about 0.5 mm wide and up to 400 mm long. It appears to have been considerably more pliable than *Daltaenia*.

It would thus seem appropriate to recognize the distinctness of the Little Dal forms from other macroscopic ribbons previously known from the Precambrian, and to assign them to a new, genus-level taxon, *Daltaenia*, characterized by a greater rigidity, and possible branching.

Genus GRYPANIA Walter, Oehler and Oehler, 1976

Type species. *Grypania spiralis* (Walcott, 1899) Walter, Oehler and Oehler, 1976.

Grypania spiralis Walter, Oehler and Oehler, 1976

Plate 39, fig. 4

- ?1872 *Arenicolites spiralis* Billings, p. 478.
 ?1886 *Montfortia filiformis* Lebesconte (partim), p. 782, pl. 34, fig. 7^{II}.
 ?1897 *Arenicolites (Spiroscolex) spirales* Dawson, p. 53, fig. 13.
 1899 *Helminthoidichnites? spiralis* Walcott, p. 236, pl. 26, figs. 5, 6.
 ?1919 Spiral impression Beer, p. 139, pl. 30. [See Note 2 added in proof, p. 353.]
 ?1971 *Arenicolites spiralis* Hofmann, p. 18, pl. 4, fig. 7.
 1976 *Grypania spiralis* (Walcott) emend. Walter, Oehler and Oehler, n. comb., pp. 877–878, pl. 2, figs. 4–10.

Description. Single, fragmentary specimen, evenly curved, unbranched carbonaceous ribbon, 13.5 mm long, 0.5 mm wide, bent into C-shaped compression 7 mm in diameter; surface smooth to finely granulate.

Occurrence. Locality 1.

Discussion. The structure fits within *G. spiralis*, whose only previously known occurrence is in the 1.3 Ga old Greyson Shale of Montana. Other possible occurrences are cited in the synonymy, and all require re-examination. They include the structure referred to *Arenicolites spiralis* by Billings (1872) and Dawson (1897) from the late Proterozoic St. John's Group of Newfoundland (see also Hofmann 1981, pl. 18). It has thus far not been possible to relocate this specimen, nor to obtain topotypes. The identity of the Newfoundland fossil thus remains unknown. If in fact it is a *Grypania*, as is suggested by the coiled shape, the Little Dal specimen would bridge the gap between the 1.3 Ga occurrence in the Belt Supergroup and that of the approximately 0.7–0.6 Ga old St. John's Group.

Genus TYRASOTAENIA Gnilevskaya, 1971

Type species. *Tyrasotaenia podolica* Gnilevskaya, 1971.

Tyrasotaenia sp.

Plate 35, fig. 10; Plate 39, figs. 9–11

Description. Compressed fragments of slender, twisted, black carbonaceous filaments, pyritized filaments, and impressions; 80–150 μ m wide, up to 7 mm long ($N = 10$); surface without ornamentation other than irregularities due to impressions of mineral grains. Specimens scattered along bedding planes, not closely crowded.

Occurrence. Localities 1 and 2.

Discussion. The carbonaceous specimens from the Mackenzie Mountains are narrower than the typical *T. podolica* from the Ukraine, but otherwise indistinguishable. They are comparable in size to specimens of *T. sp.*, cf. *T. podolica* reported from the 1.8 Ga old Tuanshanzi Formation of northern China (Hofmann and Chen, 1981), and thus provide a link between much older and younger occurrences.

Tyrasotaenia? sp.

Plate 35, figs. 4 (partim), 8 (partim), 9; Plate 36, fig. 12 (partim); Plate 37, fig. 8

Description. Very slender, somewhat tortuous, three-dimensionally preserved strings, 80–150 μ m wide, up to 10 mm long, preserved by bluish-grey weathering equigranular microcrystalline calcite identical to that filling specimens of *Tawuia* and *Chuarua* (see discussion under *Tawuia*); no unequivocal black carbonaceous envelope seen between fill and matrix. Some specimens bunched around three-dimensionally preserved *Chuarua* and *Tawuia*, with subradial orientation (Pl. 35, figs. 4, 8; Pl. 36, fig. 12).

Occurrence. Locality 1; seen only in beds with three-dimensionally preserved macrofossils.

Discussion. Except for their three-dimensional preservation and lack of carbonaceous envelope, these specimens differ neither in size nor shape from compressed specimens of *T. sp.* that are found on the same bedding surface. The absence of carbonaceous wall material separating fill from matrix is bothersome if one invokes the same taphonomic process as that used to explain the preservation of the larger fossils, in which carbonized cell-wall material remains; in this respect they are more like the nonbiogenic 'molar-tooth' structures. Nevertheless, one can suggest that, because the filaments are very much smaller, and thus probably also thinner walled than *Tawuia* and *Chuarua*, the absence of a carbonaceous envelope could be due to obliteration during diagenesis. The carbonaceous material is more likely to be preserved as a compression, because juxtaposition of opposite sides would double the thickness of carbonaceous material. In this interpretation *T.?* sp. and *T. sp.* would be two preservational variants of the same species.

Alternatively, the two taxa could be completely different phenomena, considering that the absence of a carbonaceous envelope is real and not due to removal after burial. A trace fossil interpretation comes to mind. In the light of present thinking among specialists as to what constitutes the oldest unquestionable evidence of burrowing activity, this occurrence would be anomalous. None the less, without dismissing this interpretation outright on theoretical grounds, several points are worth noting: First, the diameter of the structures is tiny, as might have been the inferred 1.1–0.7 Ga old originators, based on our present knowledge of metazoan evolution, and on the existence of microscopic, vasiform, heterotrophic protists in 0.9–0.7 Ga old rocks. Secondly, the structures are tortuous, like some of the earliest generally accepted trace fossils from the late Precambrian (e.g. *Torrowangea*, and some small *Planolites*), and they also have a general subradial orientation with respect to the macrofossils, as if the latter might have been points of attraction for exploitation. Mobility of such postulated primitive, microscopic heterotrophs in the substrate would have been facilitated by a high original sediment porosity before final compaction, as well demonstrated by the presence of crumpled plates of 'molar-tooth' structure. An argument against a trace fossil interpretation is the vague nature of the circumstantial evidence. The hypothesis can be tested, for instance, if they are ichnofossils, by finding the originator at one end, fecal pellets, or backfill structures; or if they are algal, by demonstrating that the termini of the strings are angulate, and the strings thus fragmental, or by finding strings with a carbonaceous envelope.

Another possibility is also briefly mentioned. The concentration of the strings around specimens of *Chuarua* could indicate that they were either part of the larger fossil, or that they represent saprophytic organisms growing on them, such as fungi. Smaller but similar such structures have been reported from the late Proterozoic of Asia under the name *Phycomycetes* (Timofeev 1969, pp. 27, 48, pl. 34, figs. 3, 5, 6) and *Mastigophycus* (Wang and Zhai 1982, p. 102, pl. 1, figs. 1–8). Alternatively, they were disparate taxa clumped mechanically during settling.

It thus seems that, although the nature of *Tyrasotaenia?* sp. is obscure, the interpretation as three-dimensionally preserved *T. sp.* seems adequate, despite the absence of a distinct carbonaceous wall.

Dubiofossil 'BERGAUERIA?' Hofmann, in Hofmann and Aitken, 1979

Plate 38, figs. 5–6

1979 *Bergaueria?* sp. Hofmann, in Hofmann and Aitken, p. 163, fig. 17C, D.

Description. Concentrically wrinkled circular to elliptical structures, 10–17 mm in diameter; isolated or juxtaposed, tapering, frond-like structures gradually widening distally; fronds composed of eccentric semicircular wrinkles of less than 1 mm relief. Preserved in medium- to fine-grained, laminated sandstone.

Occurrence. Locality 2.

Discussion. New specimens of this dubiofossil were collected in 1979 at the locality of the first find previously reported in Hofmann and Aitken (1979), and these include the counterpart to that found by

Aitken two years earlier, and illustrated in that report. Various attempts at interpreting these enigmatic structures included a trace fossil explanation (laterally moving coelenterates), and one as abiogenic markings, particularly dewatering or degassing structures. No firm conclusions were reached, and the structures were assigned to the dubiofossils.

In addition to the previously reported superficial resemblance to marks made by the modern jellyfish *Aurelia*, there is also a much more striking resemblance to a specimen illustrated as *Zoophycos* from the upper Palaeozoic of Montana (Rodriguez and Gutschick 1970, p. 433, pl. 7a). This structure, however, is distinct from other specimens in the assemblage which undoubtedly belong to this ichnogenus (R. C. Gutschick, pers. comm. 1984). Illustrations of other specimens of this '*Zoophycos*' kindly supplied by Gutschick show concentric patterns (just as the material from the Mackenzie Mountains), as well as cross-cutting relationships between different frond-like structures, making a nonbiologic origin more plausible. Possible mechanisms include gas bubbling through viscous mud slowly flowing subaerially down a gentle slope in hot spring areas. Such a mud pool interpretation has been advanced for Archean structures associated with a mineralized hydrothermal vent system in the Barberton greenstone belt (de Wit *et al.* 1982, fig. 7). A particularly striking photograph of such migrating gas escape vents in a modern setting in New Zealand is in Lloyd (1972, p. 98, fig. 63). However, the smoothly curved patterns in the illustration in de Wit *et al.* (1982) look also like some diffusion patterns produced by rhythmic precipitation (Liesegang phenomenon). The wrinkles in the structures from the Little Dal are not even or smooth, and thus unlike the diffusion banding and the mud pool structures, and they formed subaqueously in a basinal setting.

A more probable explanation is that they are sapping structures, due to dewatering. The concentric portions would represent vertically compacted dewatering channels, and the frond-like pattern would be small, vertically compacted collapse features that formed by progressive distal migration as failure occurred due to sapping in the underlying lamina during dewatering. The pattern is somewhat analogous to the crescentic slump scarps that progressively extend headward as slope failure occurs during landslide formation. Such slump scarps are also uneven, angulate crescents, as would be expected from tensional failure, and not smooth and even like pressure ridges that would result from flowage, in the opposite direction, of material being introduced into the deforming layer via the concentric structure.

The resemblance is thus closest to the questionable '*Zoophycos*' alluded to above. The fact that such similar structures occur in rocks separated in age by about half a billion years strongly supports the view that a nonbiologic mechanism is required for both; a sapping structure is thought to be a suitable explanation.

SUMMARY AND CONCLUSION

The Little Dal biota, dominated by *Tawuia* and *Chuaria*, provides an important glimpse of macroscopic life in the ocean about one billion years ago. The new collections here reported demonstrate that three-dimensional organisms could attain a size of at least 150×2.7 mm (after recalculating the original diameter by removing the effect of flattening). A possible biological relationship between the two taxa is suggested by their close association, by the presence of small discs attached to, or included in *Tawuia* specimens, and, possibly, by the allometric growth relationships (length/width). Evidence from other occurrences is contradictory, however, and this question remains open. The large size, the carbonaceous composition, the general shape, and the geologic age suggest that these organisms were photosynthesizing eucaryotes, probably some kind of planktonic algae.

The associated *Beltina* is also known from large fragments, at least up to 3×8 cm in size, further demonstrating the existence of large entities in the Proterozoic seas. But whether these are fragments of large thalli or compressions of procaryotic or eucaryotic mats or scums is still unresolved.

The specimens attributed to *Longfengshania*, with their apparent branching, are suggestive of relatively complex organisms, as is the questionably branching new genus *Dahtaenia*, but conclusive branching must still be demonstrated. Their size, shape, and composition again suggest probable eucaryotic algal affinities, as do the smaller *Grypania* and *Tyrasotaenia*. The latter two represent

specimens intermediate in age between previously reported occurrences, and they thus provide a link in the stratigraphic record.

Normally, the taxa are preserved as carbonaceous compressions. The extraordinary conditions leading to the three-dimensional preservation of the two dominant taxa also are responsible for the development of the 'molar-tooth' structures. Crystallization of pure equigranular microcrystalline calcite (microspar?) in both fossils and 'molar-tooth' structure was a very early diagenetic phenomenon; it occurred before compaction of the sediment, which eventually amounted to more than 50%. The nature of these unusual conditions is not known; elevated salinity or the presence of certain organic compounds may be involved, perhaps even carbonate gels.

The three-dimensionally preserved *Tyrasotaenia*?, though occurring separately, has a slight tendency to cluster around specimens of the macrofossils, particularly *Chuaria*, suggesting a possible relationship between the two: attached filaments, saprophytic organisms, or traces of tiny organisms feeding on the larger bodies; the preferred interpretation, however, is that they are clusters of independent taxa.

Studies on the Little Dal biota are continuing, and further interesting discoveries are to be expected.

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NOTES ADDED IN PROOF

1. New data relevant to the discussion of *Tawuia* became available too late for inclusion in the text on p. 342. Three additional species of *Tawuia* have been proposed: *T. suketensis* (Mathur 1982, p. 128, fig. 3B; 1983a, p. 364, fig. 1D) and *T. rampuraensis* (Mathur 1983a, p. 364, fig. 1E) from the Vindhyan of India, and *T. fusiformis* (Xing 1984, pp. 34, 115, 153, pl. 21, fig. 7) from the Sinian of southern China. Specimens illustrated all resemble short specimens of *T. dalensis*. Mathur (1983a, p. 364, fig. 1F) also proposed a new genus and species for structures apparently identical to the *T. dalensis* illustrated in Plate 36, fig. 3.

2. The name *Spiroichnus beerii* was proposed by Mathur (1983b, pp. 112–113, pl. 2, figs. 1–2) for the spiral impressions reported by Beer (1919). [See synonymy for *Grypania spiralis* on p. 349.]

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